

STUDIES ON SOME PRESUMED HYBRID POPULATIONS IN *Eucalyptus*

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ABSTRACT: Three morphologically similar but disjunct populations of *Eucalyptus*, generally morphologically intermediate between *Eucalyptus globulus* ssp. *bicostata* and *E. glaucescens*, are found in northeastern Victoria. A progeny test revealed that the seedlings of the three populations were no more variable than the seedlings of nearby populations of *E. globulus* ssp. *bicostata* and *E. glaucescens*, and less variable than the seedlings of an apparent hybrid between *E. aff. smithii* and one of the three populations. Thus it is concluded that, although there may be several reasonable alternative explanations for the origin of the three populations, they have not resulted from recent hybridization between *E. globulus* and *E. glaucescens* as had been proposed earlier, and are best regarded as component populations of an undescribed species.

INTRODUCTION

In previous papers (Parsons & Kirkpatrick 1972, Kirkpatrick, Simmons & Parsons 1973) attempts were made, through analysis of the morphology of adult populations and progeny tests, to establish the validity of the term 'phantom hybrid' in relation to several populations of *Eucalyptus*. In the case of *E. cypellocarpa* L. Johnson and *E. goniocalyx* F. Muell. ex. Miq. the presumed hybrid populations were disjunct from populations of both supposed parents. In the case of *E. globulus* Labill. and *E. cypellocarpa* one parent was found contiguous to the supposed hybrids. In this paper I attempt to discover the evolutionary and taxonomic status of three populations identified in part by Willis (1972, p. 420) as presumed hybrids of *E. glaucescens* Maiden & Blakely and *E. globulus* Labill. ssp. *pseudoglobulus* (Naudin ex Maiden) Kirkpatrick (*E. pseudoglobulus* of Willis). Only one of these three populations is contiguous with the supposed parent species, thus presenting an interesting situation for comparison.

The three populations consist of glaucous-leaved mallees similar in habit to *E. glaucescens*, but differ most markedly from *E. glaucescens* in the shape and size of the fruits, which approximate those of some populations of *E. globulus*. Population NS is situated on steep rocky slopes below Stradbroke Chasm in northeastern Victoria (Fig. 1). *E. viminalis* Labill. and *E. globulus* Labill. ssp. *bicostata* (Maiden *et al.*) Kirkpatrick are found immediately adjacent to this population in a more mesic situation, and *E. glaucescens* is found on Mt. Stradbroke above the scarp cliff

which separates it from population NS. These three species are from the same section of the same subgenus and thus are likely to be capable of hybridization (Pryor & Johnson 1971). The only other species in the same subgenus growing adjacent to population NS is *E. albens* Benth. which is in the section *Adnataria* and is thus less likely to be capable of hybridization with the other three species. Population LR is separated from population NS by a disjunction of 14 km, and is found on the rocky edge of the Little River Gorge around the lookout. The only other eucalypt in the same section as those mentioned previously and found in close vicinity to population LR is a mallee resembling *E. smithii* R.T. Bak., although glaucous-leaved populations of mallees observed on the precipitous walls of the gorge may be either *E. glaucescens* or similar to population LR. Population MW is found on steep rocky slopes around the summit of Mt. Wheeler, intermingled with *E. aff. smithii*, and with a small stand of *E. viminalis* in the near vicinity. A disjunction of 2½ km separates MW and LR (Fig. 1). Thus, none of the four species which could be suspected to have some role in their genesis are found near all of the three populations (Table 1).

E. viminalis, a species found in many hybrid combinations, is believed on the basis of field, morphological and progeny evidence to cross with both *E. glaucescens* and *E. globulus* (Pryor 1951, 1962). There seems to be no similarly substantiated reports of any other combinations of the four species (including *E. aff. smithii*) in the literature.

Careful field examination of the form, leaves, in-

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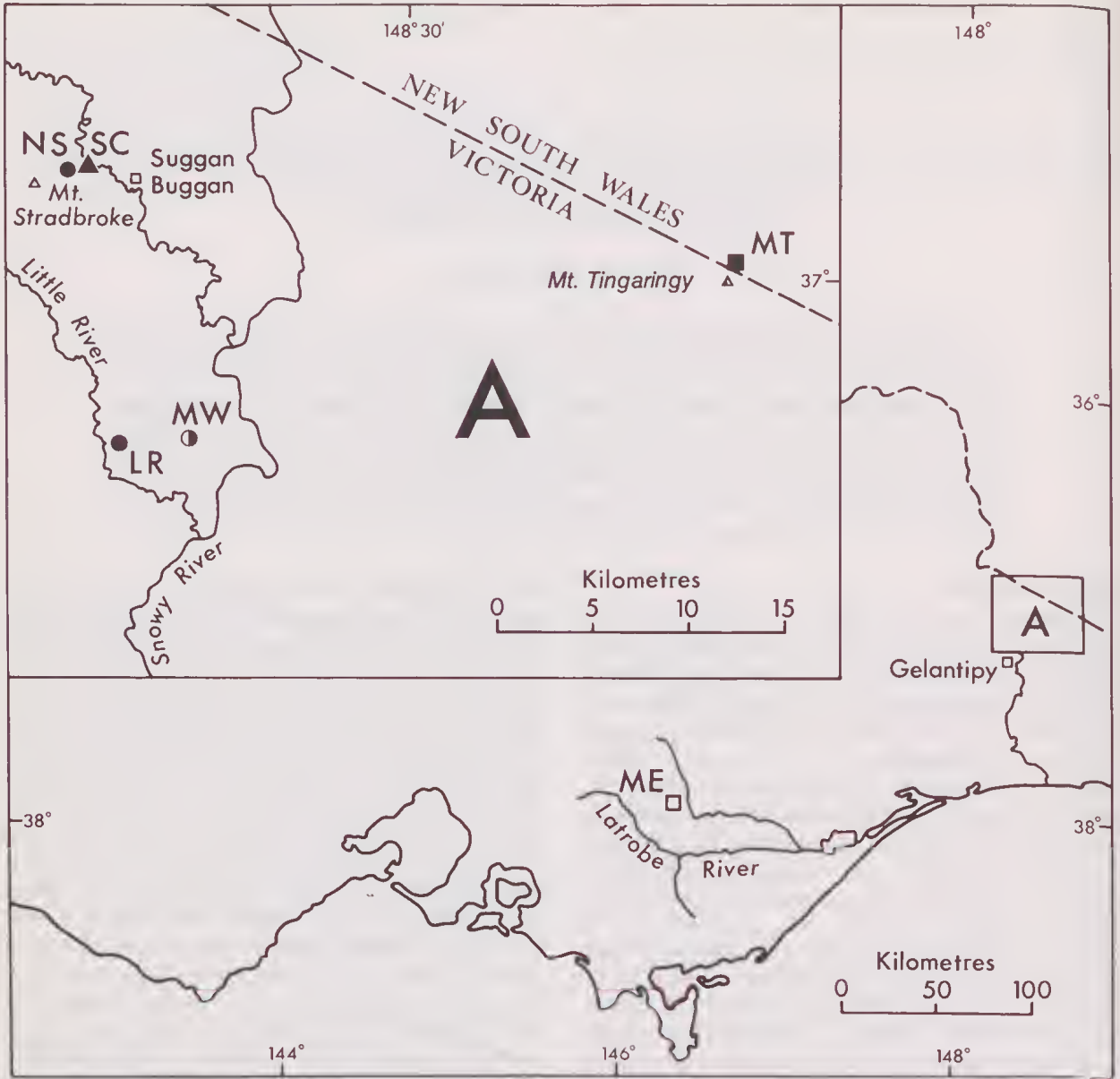


Fig. 1. The location of the sampled populations.

florescences, buds and fruits of populations NS, LR and MW, revealed *E. viminalis* and *E. aff. smithii* to be unlikely parents. The main piece of evidence that led to this conclusion was fruit size, as the fruits of trees in the three populations are invariably larger than those found on either *E. viminalis* or *E. aff. smithii*, and are also larger than all except the southern Victorian populations of *E. glaucescens*. To produce the buds and adult leaves found in the three populations *E. glaucescens* would be necessarily involved, thus necessitating another parent species with fruits larger than both *E. glaucescens* and the three populations. *E.*

globulus ssp. *bicostata* fulfils this requirement. The nearest stand of *E. globulus* ssp. *pseudoglobulus* is at Gelantipy (Fig. 1) and as this taxon is generally confined to more equable climates than those found in the study area (Kirkpatrick 1975) and as its fruits are generally no larger than those of the three populations, it seemed a less likely parent than *E. globulus* ssp. *bicostata*. Thus, subsequent work was designed to test whether the three populations resulted from hybridization between *E. glaucescens* and *E. globulus* ssp. *bicostata*. Also considered was the role of *E. aff. smithii* in contributing to the variability of populations

TABLE 1
THE POPULATIONS SAMPLED

| Symbol | Taxon | Location | Associated taxa in same section |
|--------|--|--|---|
| NS | — | On steep slopes below Stradbroke Chasm | <i>E. glaucescens</i> (adjacent, not mixed), <i>E. viminalis</i> , <i>E. globulus</i> ssp. <i>bicostata</i> |
| MW | — | Rocky slopes near summit of Mt. Wheeler | <i>E. aff. smithii</i> , <i>E. viminalis</i> (adjacent, not mixed) |
| LR | — | Southern edge of Little River Gorge near lookout | <i>E. aff. smithii</i> |
| ME | <i>E. glaucescens</i> | Southeastern slopes of Mt. Erica | <i>E. nitens</i> Maiden |
| MT | <i>E. glaucescens</i> | Mt. Tingaringy | — |
| SC | <i>Eucalyptus globulus</i> ssp. <i>bicostata</i> | Alongside stream below Stradbroke Chasm | <i>E. viminalis</i> , population NS |

LR and MW, as a few trees in these populations exhibited some intermediacy in the adult phenotype with this species.

METHODS

Adult Morphology: Collections of leaves, fruits, seed and buds when available were made from a variable number of trees (Table 2) from two populations of *E. glaucescens* (ME, MT), one population of *E. globulus* ssp. *bicostata* (SC) and populations NS, LR and MW. One tree of *E. aff. smithii* (SM) was sampled along with an apparent hybrid (LR2) between it and population LR. Sampling of all populations took place within areas less than 0.5 km in diameter.

To assess the range of variation within *E. glaucescens* specimens were obtained from the National Herbaria of New South Wales and Victoria, the Forest

Research Institute Herbarium, and the Herbarium of the University of Tasmania, patterns of geographic variation in *E. globulus* having been already investigated (Kirkpatrick 1975). Twenty measurements per sampled tree or herbarium specimen were made of maximum fruit diameter, diameter at the calycine ring, fruit height, height of the fruit above the calycine ring, number of valves per fruit, and pedicel and peduncle length. The trees were classified using the polythetic agglomerative computer program HGROU which groups on the basis of a generalized distance function (Vendman 1967). The attributes used were those shown in Table 2 with the exception of seed weight. The figures for each attribute were normalized prior to the classificatory process to ensure that each variable was equally weighted in the analysis.

The weight of fifty seeds from each collected specimen was measured on an electric balance. Population

TABLE 2
POPULATION MEANS AND COEFFICIENTS OF VARIATION FOR ADULT MORPHOLOGY

| Character | SC(8)*** | | NS(11) | | MW(13) | | LR(10) | | ME(9) | | MT(10) | |
|--|----------|------|--------|------|--------|------|--------|-------|-------|------|--------|------|
| | M* | CV** | M | CV | M | CV | M | CV | M | CV | M | CV |
| Maximum fruit diameter (mm) | 16.2 | 7.7 | 12.1 | 7.3 | 10.3 | 10.9 | 9.5 | 7.75 | 8.9 | 6.6 | 7.0 | 5.8 |
| Fruit height/maximum diameter | 0.85 | 6.4 | 0.82 | 7.2 | 0.90 | 8.8 | 0.96 | 10.2 | 1.09 | 6.4 | 1.14 | 5.3 |
| Maximum diameter/diameter at the calycine ring | 1.00 | 0.0 | 1.00 | 0.0 | 1.00 | 0.0 | 1.00 | 0.0 | 1.13 | 5.3 | 1.05 | 2.6 |
| Height of the fruit above the calycine ring (mm) | 3.65 | 22.8 | 1.22 | 45.1 | 1.84 | 26.7 | 1.16 | 43.5 | 0.05 | 94.6 | 0.45 | 63.4 |
| Pedicel height (mm) | 0.0 | 0.0 | 0.32 | 57.0 | 0.60 | 41.1 | 0.33 | 118.5 | 0.25 | 67.4 | 0.24 | 28.4 |
| No. of valves per fruit | 3.91 | 4.1 | 3.89 | 6.9 | 4.01 | 3.8 | 3.93 | 5.8 | 3.29 | 5.3 | 3.21 | 5.1 |
| Peduncle length (mm) | 2.88 | 32.6 | 4.15 | 21.4 | 3.43 | 21.9 | 3.88 | 23.1 | 2.88 | 22.7 | 2.59 | 16.2 |
| Weight of 50 seeds (g) | 0.105 | 15.9 | 0.069 | 20.8 | 0.056 | 20.2 | 0.050 | 25.4 | 0.092 | 17.8 | 0.067 | 18.3 |

* Mean

** Coefficient of variation (%)

***Number of individuals in sample

means and coefficients of variation were calculated for seed weight and the characters used in the classificatory analysis.

Progeny Test: Seed from eight trees each of populations ME, MT, NS, LR, MW and SC and from one tree of *E. aff. smithii* and the apparent hybrid of *E. aff. smithii* and population LR were stratified for four weeks then placed in germinating dishes. The seed from most trees of ME and one tree of MT failed to germinate. Sixteen newly germinated seedlings per tree were planted in an equal mixture of sand and *Sphagnum* (one seedling per pot) in three totally randomized blocks in a heated glasshouse. Water and nutrients were held near optimum amounts at all times. After 12 weeks, seedling height, seedling length (many seedlings were prostrate), the number of leaf pairs, the number of secondary growth nodes, and the length and maximum breadth of one of the first, third and fifth leaf pairs above the cotyledons were measured. Tree means and coefficients of variation were calculated for the characters shown in Table 3.

RESULTS

Adult Morphology: The anomalous populations (NS, MW and LR) were completely intermediate between SC and the *E. glaucescens* populations (ME and

MT) in maximum fruit diameter and height of the fruit above the calycine ring. In all other measured characters intermediacy was at least partially lacking (Table 2). Only in the ratio fruit height/maximum fruit diameter and in seed weight were the coefficients of variation for all three anomalous populations greater than those for both SC and the *E. glaucescens* populations (Table 2). Although tree means of *E. globulus*, *E. glaucescens* and the anomalous populations overlapped in most measured adult characters, a combination of characters could easily be used to separate the three groups of populations (Table 2).

The classificatory analysis placed all trees of *E. glaucescens* in a distinct group, in which the southern Victorian trees including population ME were concentrated in two of the groups at the ten group level of agglomeration (Fig. 3). The anomalous populations were fused into a small group which included the single specimen of *E. aff. smithii* and the supposed hybrid (LR2) of this species with population LR, and a larger group which included the single relatively small-fruited specimen of *E. globulus* ssp. *bicostata* apparent in Fig. 2. The remaining seven specimens of *E. globulus* formed a distinct group which amalgamated with the anomalous population group in the next to last fusion (Fig. 3).

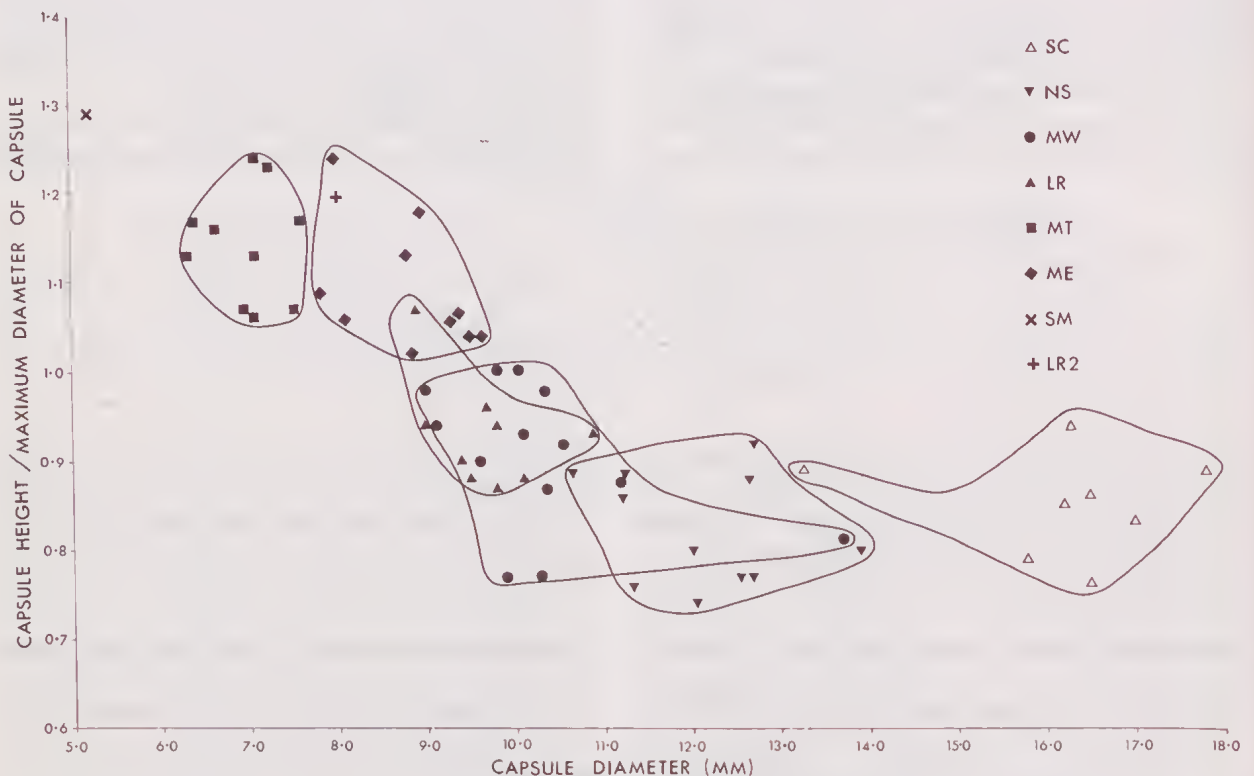


Fig. 2. Scatter diagram of tree means of maximum fruit diameter and fruit height/maximum fruit diameter.

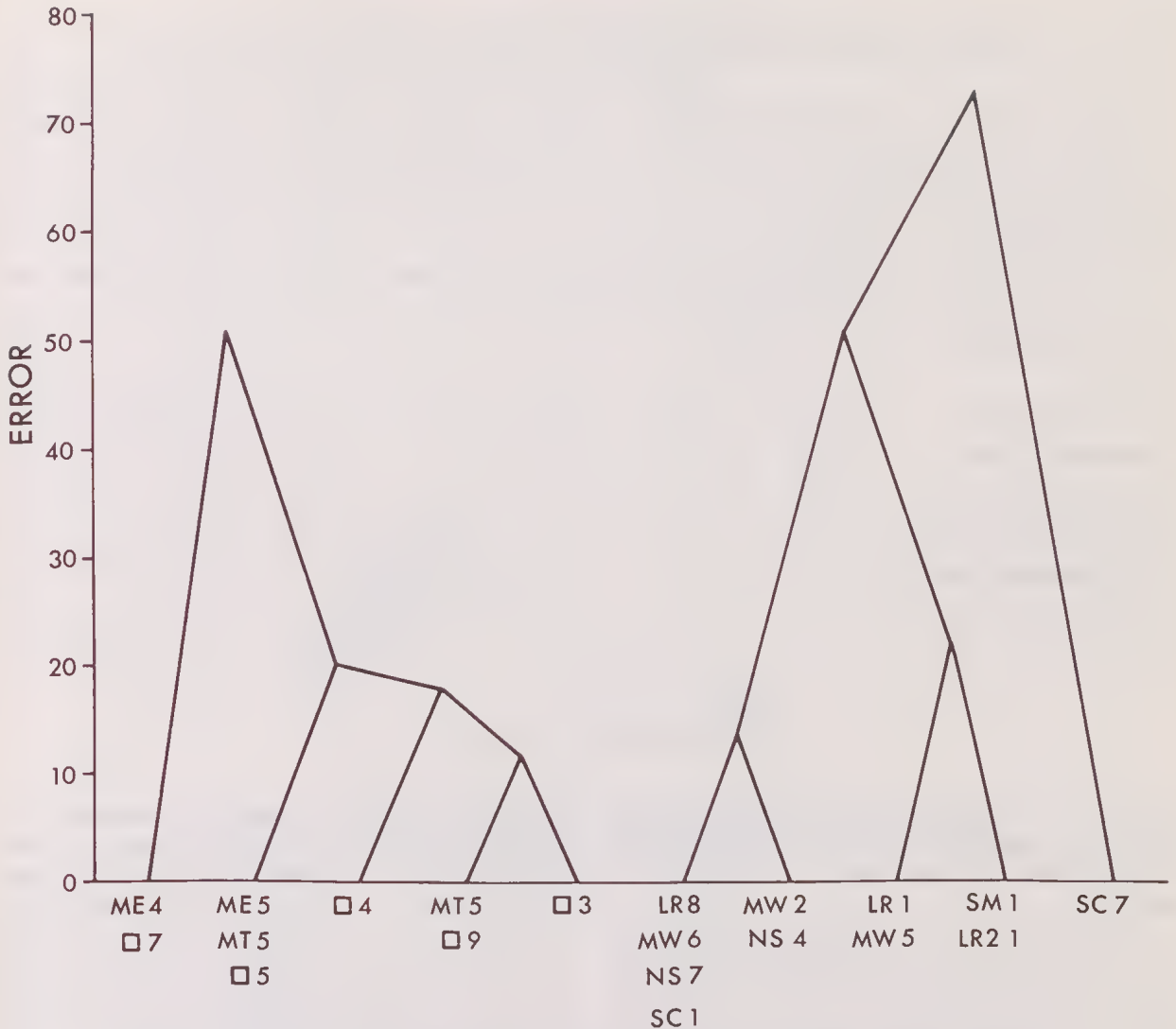


Fig. 3. Dendrogram from HGROU analysis. Agglomeration is shown from the ten group level upward, the composition of each group being shown below the dendrogram. Empty squares symbolize herbarium specimens of *E. glaucescens*.

Progeny Test: The progeny of the anomalous populations proved to be intermediate between the progeny of population MT and the progeny of population SC in all but three growth characters (Table 3, Figs. 4, 5). The lack of intermediacy in these characters may be due to the experimental conditions being more suitable for these populations than for either MT or SC, and other experimental conditions could give different results.

The progeny of the supposed hybrid (LR2) between population LR and *E. aff. smithii* was intermediate between its putative parents in all characters except leaf length in the first pair above the cotyledons and the angle of the main stem with the ground surface (Table 3). The supposed hybrid progeny had higher coeffi-

cients of variation than either putative parents in all except four characters. In contrast, in only one character were the coefficients of variation of all three anomalous populations higher than those of both populations SC and MT, and in three characters the progeny of the three populations had coefficients of variation lower than both SC and MT (Table 3).

DISCUSSION

Although the anomalous populations are generally intermediate between *E. globulus* ssp. *bicostata* and *E. glaucescens* in their seedling characteristics, they are only partially intermediate between these two taxa in their adult morphology. NS, MW and LR are no more variable in adult and juvenile characteristics than

TABLE 3
CHARACTER MEANS AND MEAN COEFFICIENTS OF VARIATION FOR FIVE POPULATIONS AND
THE PROGENY OF TWO TREES

| Character | SC(8)* | | NS(8) | | MW(8) | | LR(8) | | MT(7) | | LR2(1) | | SM(1) | |
|---|--------|-------|-------|------|-------|------|-------|------|-------|------|--------|------|-------|------|
| | M** | CV*** | M | CV | M | CV | M | CV | M | CV | M | CV | M | CV |
| Seedling length (cm) | 16.5 | 18.0 | 23.4 | 17.1 | 26.1 | 15.7 | 25.3 | 14.6 | 17.3 | 20.5 | 25.2 | 26.2 | 22.0 | 18.6 |
| Angle of main stem with ground surface (°) | 87.8 | 7.3 | 44.4 | 51.6 | 48.4 | 51.7 | 43.7 | 55.3 | 32.8 | 62.1 | 65.8 | 45.4 | 56.3 | 51.8 |
| No. of open leaf pairs | 7.1 | 13.3 | 10.1 | 10.8 | 9.9 | 12.2 | 10.5 | 12.0 | 9.9 | 14.1 | 8.7 | 14.4 | 8.4 | 9.0 |
| No. of secondary growth shoots | 0.3 | 199.3 | 4.5 | 46.9 | 5.0 | 49.1 | 5.9 | 48.0 | 5.5 | 42.4 | 8.9 | 35.9 | 9.4 | 40.3 |
| Leaf length 1st pair | 3.9 | 15.85 | 2.3 | 16.6 | 2.6 | 16.1 | 2.5 | 15.8 | 2.0 | 17.6 | 2.9 | 30.6 | 2.4 | 24.1 |
| Leaf length 3rd pair | 7.1 | 13.3 | 3.0 | 12.9 | 3.3 | 12.7 | 3.1 | 12.1 | 2.8 | 17.4 | 4.0 | 12.8 | 4.3 | 12.4 |
| Leaf length 5th pair | 6.3 | 17.4 | 2.5 | 14.6 | 2.7 | 15.5 | 2.6 | 19.7 | 2.2 | 20.8 | 3.8 | 17.3 | 4.5 | 21.8 |
| Leaf length/breadth 1st pr | 3.4 | 17.4 | 1.9 | 24.9 | 2.1 | 24.7 | 2.4 | 28.4 | 1.9 | 23.5 | 3.0 | 19.3 | 3.5 | 15.2 |
| Leaf length/breadth 3rd pr | 2.6 | 11.7 | 1.1 | 14.7 | 1.2 | 13.9 | 1.4 | 16.5 | 1.0 | 22.8 | 2.2 | 24.8 | 2.8 | 22.4 |
| Leaf length/breadth 5th pr | 2.2 | 15.2 | 0.9 | 11.6 | 0.9 | 10.3 | 1.0 | 14.7 | 0.7 | 19.7 | 2.1 | 29.0 | 2.6 | 24.3 |

* No. of parent trees

** Mean

***Mean of coefficients of variation (%)

SC and MT. In fact, in juvenile characteristics, MT, the type population of *E. glaucescens*, was clearly the most variable of all populations included in the experiment.

LR2 was clearly intermediate between population LR and *E. aff. smithii*, and in most juvenile characters measured was more variable than either of its supposed parents. This intermediacy and high variability was also evident in characters not recorded in the results of this study. For instance, LR2 varied between 3 and 7 in flower number per inflorescence. Population LR has consistently three flowers per inflorescence and *E. aff. smithii* has seven flowers per inflorescence. Also, the progeny of *E. aff. smithii* was non-glaucous, that of LR was glaucous, and that of LR2 was mixed. Thus, there is extremely strong evidence that population LR and *E. aff. smithii* hybridize.

The contrast between the relatively high coefficients of variation found for LR2 and the relatively low coefficients of variation found for populations NS, MW and LR, and the lack of intermediacy in these populations recorded above, suggest that recent active hybridization is not occurring between *E. globulus* ssp. *bicostata* and *E. glaucescens* to produce the anomalous populations. However, there is some evidence to suggest that gene-exchange with contiguously occurring species has influenced the morphological charac-

teristics of the three populations. Population NS is closer in most characteristics to *E. globulus* ssp. *bicostata* than MW or LR. Population LR is closer in most characteristics to *E. aff. smithii* than NS or MW. Population MW tends to be closer to *E. aff. smithii* than population NS, but its *E. aff. smithii* tendencies may have been tempered somewhat by gene-exchange with *E. viminalis*. Thus, the similarities of each of the three populations reflect the relative distributions of *E. globulus* ssp. *bicostata*, *E. aff. smithii* and *E. viminalis* (Table 1).

The mode of origin of the anomalous populations is uncertain. The likelihood that the three populations evolved through selection from *E. glaucescens* seems low, given the overall similarity of their environments. However, they may be the remnants of a stabilized hybrid swarm of *E. globulus* and *E. glaucescens* further influenced by gene-exchange with *E. viminalis* and *E. aff. smithii*. Alternatively, NW, MW and LR may be relic stands of a formerly more extensively distributed species, stranded on a few steep rocky slopes in the course of climatic change.

Although the three populations differ somewhat in their morphological characteristics, they can be easily distinguished as a group from all closely related populations, they breed true, and each population has a spatial reality. Thus, taxonomically they are best re-

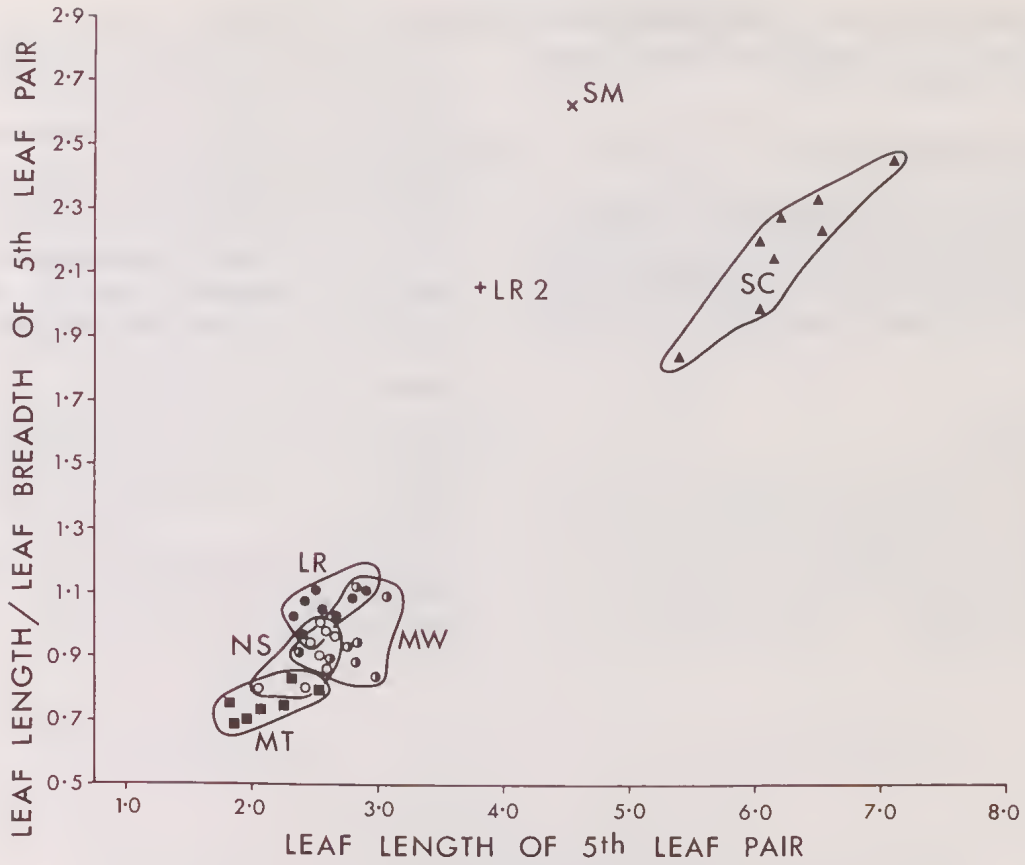


Fig. 4. Scatter diagram of means of leaf length in the fifth leaf pair above the cotyledon and leaf length/leaf breadth in the fifth leaf pair.

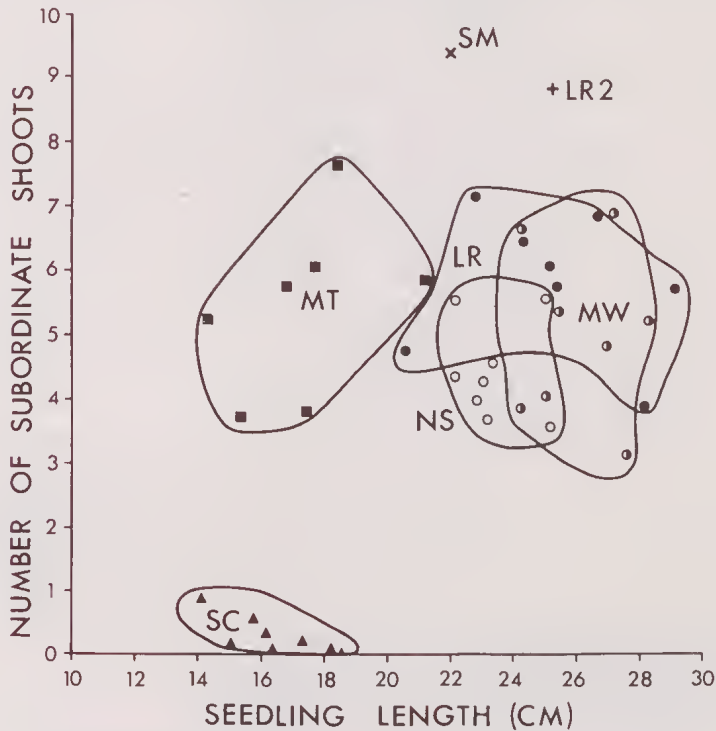


Fig. 5. Scatter diagram of means of number of subordinate shoots and seedling length.

garded as three populations of an undescribed species. This species is to be formally described elsewhere (Kirkpatrick & Brooker 1977).

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